
EMBRYOLOGY OF *TAKHTAJANIA* (WINTERACEAE) AND A SUMMARY STATEMENT OF EMBRYOLOGICAL FEATURES FOR THE FAMILY¹

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ABSTRACT

We present the first report on the embryology of *Takhtajania*. By adding its data to those already known from other Winteraceae (*Drimys*, *Pseudowintera*, *Tasmannia*, and *Zygogynum* s.l.), we summarize embryological features of the family to evaluate the proposed basal position of *Takhtajania* in the family and a possible sister-group relationship between Winteraceae and Canellaceae, which were recently suggested by molecular evidence. Comparisons within and between the families showed that *Takhtajania* agrees well with other Winteraceae embryologically, having no distinct features to support its basal position in the family. Although Winteraceae and Canellaceae share a number of basic embryological features, including an exotestal seed coat, Winteraceae are clearly distinct by virtue of the following features: the outermost one of the middle layers and even part of the connective tissue in the anther developing fibrous thickenings at anthesis; ovules anatropous (not campylotropous as in Canellaceae); the micropyle formed by the inner integument alone (rather than by two integuments as in Canellaceae); an exostome formed after fertilization; a persistent micropylar part of the tegmen composed of variously enlarged, thick-walled cells; and the exotesta palisadal. Winteraceae are thus a well-defined group embryologically and, despite their modern widespread distribution, genera show little diversification in embryological characters.

Key words: Canellaceae, embryology, systematic anatomy, *Takhtajania*, Winteraceae.

The Winteraceae are a relatively small woody dicotyledonous family, comprising about 65 species assigned to *Drimys*, *Pseudowintera*, *Takhtajania*, *Tasmannia*, and *Zygogynum* sensu lato (including *Belliolum*, *Bubbia*, and *Exospermum*). They are broadly distributed from the Philippines to Tasmania and New Zealand, South and Central America, and Madagascar (Vink, 1993). Because of its relict Gondwanan distribution as well as its distinctive primitive-type floral morphologies, the family has long attracted the attention of researchers of plant evolution and morphology. Within the family, *Takhtajania*, comprising the only extant species *T. perrieri* (Capuron) Baranova & J.-F. Leroy in the Africa/Madagascar region, has been considered most isolated, and in fact it differs from the three other genera in having flowers with two carpels united to a paracarpous gynoecium, instead of free carpels or a number of carpels united to a eusyncarpous gynoecium. *Takhtajania* thus has been placed in a subfamily of its own, Takhtajanioideae, and the other genera in another subfamily Winteraceae (Leroy, 1978; Takhtajan, 1997).

Takhtajania has been very poorly understood in general with respect to its morphological and evolutionary traits because only a single collection made in 1909 had been available for research until recent times (Leroy, 1980). A number of trees were, however, rediscovered at the Anjahanaribe-Sud Special Reserve (14°45'S, 49°29'E) in Madagascar in 1994 (see Schatz et al., 1998; Schatz, 2000 this issue). An extensive collection was subsequently made for morphological, anatomical, cytological, and molecular studies (for many results, see other articles in this *Annals* issue).

In this paper we present the embryology of *Takhtajania*, which has not been studied before. Taking the data from this study together with those from the four other genera (*Drimys*, *Pseudowintera*, *Tasmannia*, and *Zygogynum* s.l.), which have already been studied relatively well, we will summarize embryological features of the whole family Winteraceae. Molecular evidence based on combined sequence data from mitochondrial *atp1* and *matR*, plastid *atpB* and *rbcL*, and nuclear 18S rDNA has revealed that Winteraceae are sister to Canellaceae

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with support of 100% bootstrap value, and that *Takhtajania* has a basal position within the Winteraceae (Qiu et al., 1999). We will discuss whether or not the sister-group relationship between Winteraceae and Canellaceae is supported, whether or not the basal position of *Takhtajania* in Winteraceae is supported, and how Winteraceae are a coherent group distinct from the Canellaceae.

MATERIALS AND METHODS

Flower buds and fruits of *Takhtajania perrieri* in various stages of development were collected at the Anjahanaribe-Sud Special Reserve in Madagascar (vouchers: *Rakotomalaza et al.* 1342, *Schatz* 3748, *Ravelonarivo s.n.* in 1998; all at MO) and fixed with FAA (five parts stock formalin; five parts glacial acetic acid; 90 parts 50% ethanol). Twenty-eight flower buds, four open flowers, and 17 fruits were dehydrated through a *t*-butyl alcohol series, embedded in Paraplast (melting point 57–58°C), and sectioned using a rotary microtome following standard paraffin methods. Sections cut at about 6–10 μm thickness were stained with Heidenhain's haematoxylin, Safranin-O, and FastGreen FCF, and mounted with Entellan. To examine their fine structure, several anthers were embedded in Spurr's resin after dehydration through an acetone series and sectioned with glass knives using an ultramicrotome. Sections cut at about 1–2 μm thickness were stained with Toluidine blue O.

OBSERVATIONS

ANTHERS AND MICROSPORES

The small anther is supported by a more or less laminar filament (Fig. 1), and is tetrasporangiate (Figs. 2, 3). Prior to maturation the anther comprises 5 to 6 cell-layers: an epidermis, an endothecium, 2 to 3 middle layers, and a tapetum (Fig. 7). Because of the lack of younger flower buds, it is not certain how the anther wall developed. The tapetum is glandular, and its cells are 2-nucleate (Fig. 4). During maturation, the epidermal cells are enlarged to some extent but nearly collapsed eventually, and the endothecium develops fibrous thickenings (Figs. 8, 9). The middle layers mostly degenerate, but like the endothecium, the outermost layer usually develops fibrous thickenings (Figs. 8, 9). Part of the connective tissue may also develop fibrous thickenings (Fig. 8). Anther dehiscence takes place by longitudinal slits, with each slit common to two microsporangia of a theca (Fig. 9).

Meiosis in the microspore mother cell is accompanied by simultaneous cytokinesis (Fig. 5). The

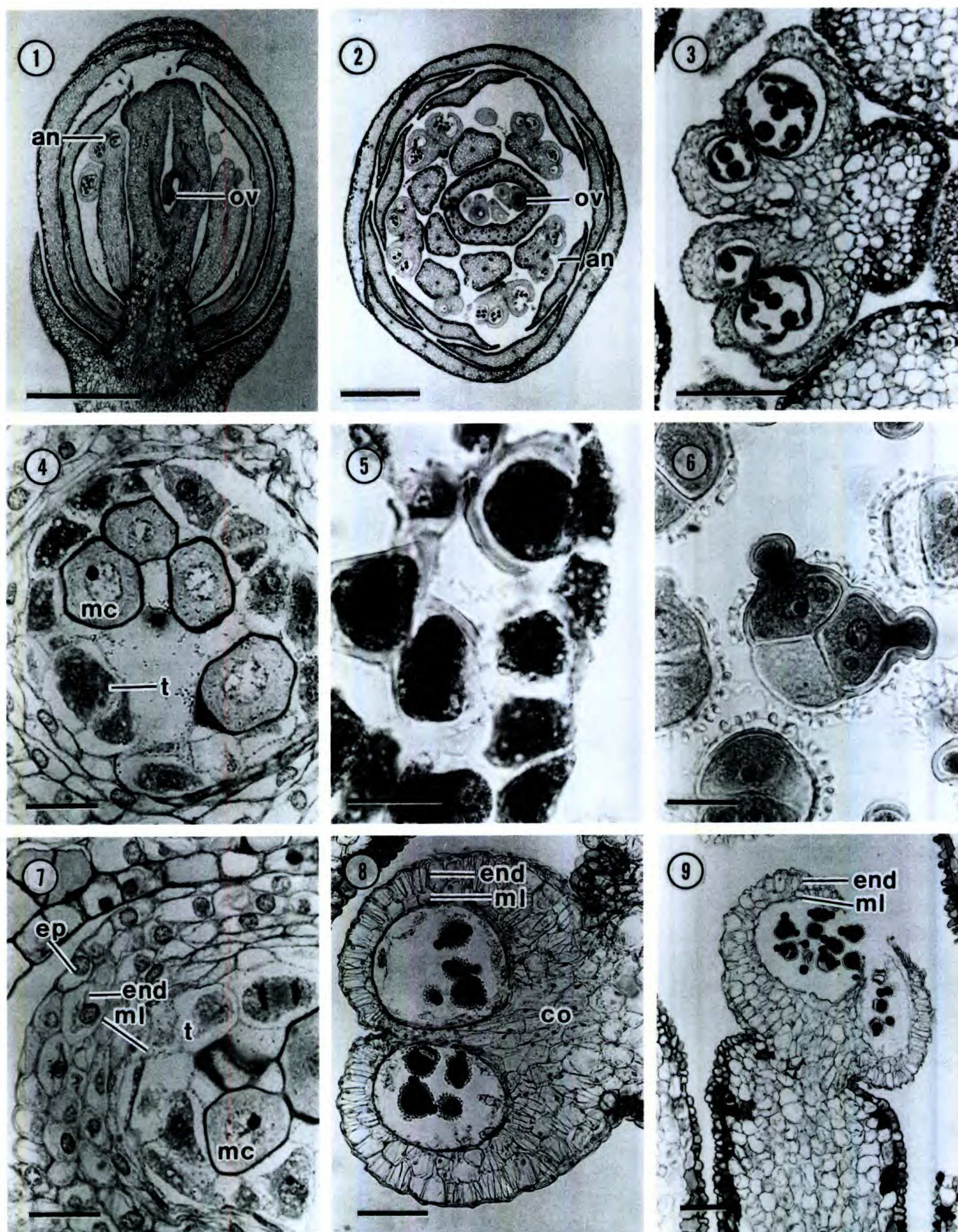
shape of resultant tetrads is tetrahedral. Unfortunately, no buds could be sectioned that would have showed stages in the division of the 1-celled microspores leading to the formation of vegetative (tube) and generative cells. Two different types of division have been found. In the synchronous type, which occurs in *Tasmannia* and *Zygogynum* s.l., the nuclei of all four pollen grains within a tetrad are at exactly the same stage of mitotic division because there are cytoplasmic connections through gaps in their internal walls. However, in the asynchronous type, which occurs in *Drimys* and *Pseudowintera*, division of the microspore nuclei is asynchronous because there are no gaps in the internal walls of each tetrad at this time (Sampson, 1981; Prakash et al., 1992). It has been suggested that the asynchronous type has evolved from the synchronous, and in view of the basal position of *Takhtajania* it would therefore be of interest to know if it too has the synchronous type of pollen mitosis.

Pollen grains are 2-celled at the time of shedding (Fig. 6).

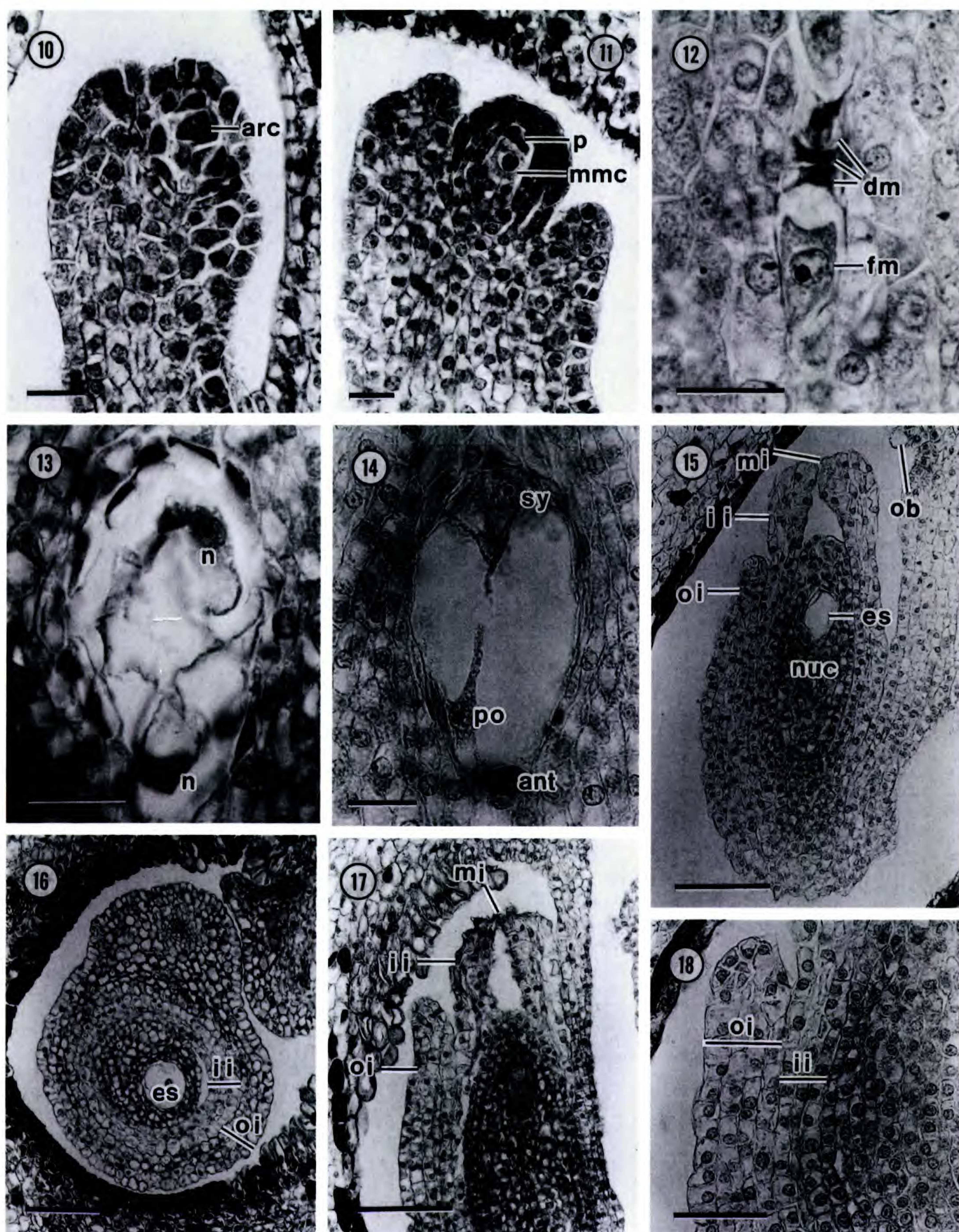
OVULES, NUCELLUS, AND MEGAGAMETOPHYTE

Early in development six to seven ovules with a long funicle are pendulous in an ovarian locule (Figs. 1, 2; see also Endress et al., 2000 this issue). They are anatropous at maturity (Fig. 15) and crassinucellate. The archesporium is 1-celled (Fig. 10). The archesporial cell divides periclinally to form the primary parietal cell above and the primary sporogenous cell below (Fig. 11). While the primary parietal cell further divides periclinally into more cells, the primary sporogenous cell develops into a megaspore mother cell. Thus ovules have one enlarged megaspore mother cell below a longitudinal row of five to six parietal cells. The megaspore mother cell undergoes meiosis to produce a linear tetrad of megaspores (Fig. 12). In the megaspore tetrad the chalazal megaspore functions (Fig. 12) and develops successively into a 2-, 4- (Fig. 13), and 8-nucleate embryo sac. Thus the mode of the embryo sac development is of the Polygonum type. An organized embryo sac has eight nuclei in seven cells: an egg cell, two synergids, two polar nuclei, and three antipodal cells (Fig. 14). The organized embryo sac is ellipsoid in shape and positioned at the upper region of the nucellus (Fig. 15). The antipodals degenerate before or soon after fertilization (Fig. 14).

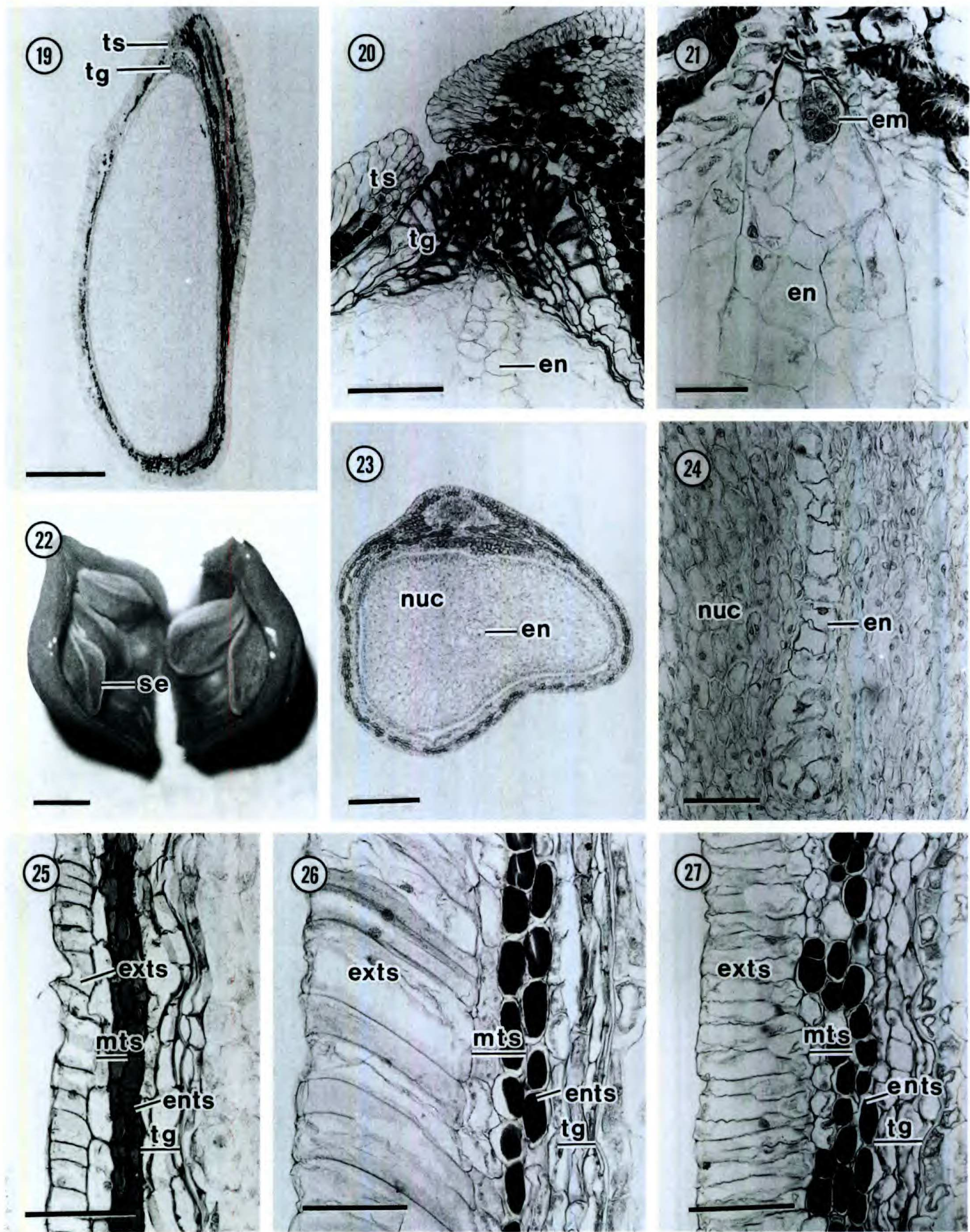
During megasporogenesis and megagametogenesis, some apical epidermal cells of the nucellus divide periclinally to form a 2-cell-layered nucellar



Figures 1–9. Development of anther and microspores in *Takhtajania*. —1. Longitudinal section (LS) of flower showing a small anther. —2. Transverse section (TS) of flower showing dehiscing anthers. —3. TS of anther. —4. TS of microsporangium showing 2-nucleate glandular tapetal cells. —5. Meiosis in microsporangium showing simultaneous cytokinesis. —6. Microtome sections of 2-celled mature pollen grains in tetrad. —7. Microtome section of young anther showing wall structure. —8. TS of older anther showing that fibrous thickenings develop in the outermost one of middle layers and even in part of the connective tissue as well as in the endothecium. —9. Microtome section of dehiscing anther. Abbreviations: an, anther; co, connective tissue; end, endothecium; ep, epidermis; mc, microspore mother cell; ml, middle layer; ov, ovule; t, tapetum. Scale bar equals 1 mm in Figs. 1 and 2, 100 μ m in Figs. 3, 8, and 9, and 20 μ m in Figs. 4–7.



Figures 10–18. Development of nucellus, embryo sac, and integuments in *Takhtajania*. —10. Longitudinal section (LS) of ovule primordium. —11. LS of young ovule with a megaspore mother cell. —12. LS of young ovule showing a linear tetrad of megaspores, in which the chalazal megaspore is functional and the other megaspores are degenerating. —13. LS of older ovule with a 4-nucleate embryo sac, showing only two nuclei in photo. —14. LS of mature ovule with an organized embryo sac, showing one synergid, (fused) polar nuclei, and one antipodal cell in photo. —15. LS of nearly mature ovule showing the micropyle formed by the inner integument alone. —16. Transverse section of mature ovule. —17. LS of mature ovule showing the micropylar part. —18. LS of mature ovule showing the thickness of integuments. Abbreviations: ant, antipodal cell; arc, archesporial cell; dm, degenerating megaspore; es, embryo sac; fm, functional megaspore; ii, inner integument; mi, micropyle; mmc, megaspore mother cell; n, nucleus of embryo sac; nuc, nucellus; ob, obturator; oi, outer integument; p, parietal cell; po, polar nucleus; sy, synergid. Scale bar equals 500 μm in Fig. 18, 100 μm in Figs 15–17, and 20 μm in Figs. 10–14.



Figures 19–27. Development of seeds and seed coats in *Takhtajania*. —19. Longitudinal section (LS) of older seed. —20. Micropylar part in LS of older seed. —21. LS of older seed showing a globular proembryo and cellular endosperm. —22. Nearly mature fruit opened artificially. —23. Transverse section (TS) of young seed. —24. LS of young seed showing cellular endosperm. —25. LS of young seed coat. —26. LS of nearly mature seed coat. —27. TS of nearly mature seed coat. Abbreviations: em, proembryo; en, endosperm; ents, endotesta; exts, exotesta; mts, mesotesta; nuc, nucellus; se, seed; tg, tegmen; ts, testa. Scale bar equals 1 mm in Fig. 19, 3 mm in Fig. 22, 200 μ m in Figs. 20 and 21, 100 μ m in Figs. 23, 26, and 27, and 50 μ m in Fig. 25.

Table 1. Comparisons of *Takhtajania* with other Winteraceae and Canellaceae in embryological characters.

Characters	Canellaceae	<i>Takhtajania</i>	Other Winteraceae ⁶
Anthers and microspores			
Number of sporangia	4	4	4
Thickness of anther wall	5 cell-layered	5 or 6 cell-layered	5 or 6 cell-layered
Mode of wall formation	?	?	Basic
Anther epidermis	Persistent	Collapsed	Collapsed
Endothecium	Fibrous	Fibrous	Fibrous
Middle layers	Crushed	Crushed except fibrous outer cell-layer	Crushed except fibrous outer cell-layer
Tapetum	Glandular	Glandular	Glandular
Number of nuclei in tapetal cell	2–4, fused	2	2 (or more), fused
Cytokinesis in meiosis	Simultaneous	Simultaneous	Simultaneous
Shape of microspore tetrads	Tetrahedral	Tetrahedral	Tetrahedral
Mature pollen	2-celled	2-celled	2-celled
Ovules, nucellus, and megagametophyte			
Ovule orientation	Campylotropous ¹	Anatropous	Anatropous
Hypostase	Not formed	Not formed	Not formed
Number of archesporial cells	1	1	1
Nature of nucellus	Crassinucellate	Crassinucellate	Crassinucellate
Thickness of parietal tissue	?	5–6 cells thick	2–5 cells thick
Mode of embryo sac forma- tion	Polygonum	Polygonum	Polygonum
Antipodal cells	Ephemeral	Ephemeral	Ephemeral
Nucellar cap	Not formed	2 cells thick	2–3 cells thick
Nucellar tissue in mature ovule	Present	Present	Present
Obturator	?	Present	Rarely present ⁷
Integuments			
Number of integuments	2	2	2
Thickness of ii (early stage)	?	3(–4) cell-layered	2(–3) cell-layered
Thickness of ii (late stage)	3 cell-layered	3(–4) cell-layered	2(–3) cell-layered
Thickness of oi (early stage)	?	4–5 cell-layered	3(–4) cell-layered
Thickness of oi (late stage)	4–8 cell-layered	4–5 cell-layered	3(–4) cell-layered
Vascular bundles	?	Absent	Absent
Micropyle formation	By ii and oi	By ii	By ii ⁸
Endothelium	Not formed	Not formed	Not formed
Endosperm and embryo			
Mode of endosperm formation	?	<i>ab initio</i> Cellular	<i>ab initio</i> Cellular
Type of embryogeny	?	?	Unknown, irregular type (<i>Drimys winteri</i>)
Seed and seed coat			
Cells of endostome after fer- tilization	Unspecialized	Persistent, thick-walled; outermost cells enlarged	Persistent, thick-walled; outermost cells enlarged
Pachychalazy	No (except <i>Cinnamosma</i>) ²	No	No
Aril/wing	Not formed ³	Not formed	Not formed
Endosperm in mature seed	Copious, ruminant ⁴	Copious	Copious
Type of seed coat	Exotestal ⁵	Exotestal	Exotestal
Thickness of testa	?	4–5 cell-layers thick	4–6 cell-layers thick
Cells of exotesta	Lignified ⁵	Lignified, palisadal	Lignified, palisadal
Cells of mesotesta	Unspecialized or oily idio- blasts	Rectangular, tanniniferous	Little specialized
Cells of endotesta	Unspecialized	Rectangular, tanniniferous	Unspecialized, crushed
Cells of tegmen	Crushed	Unspecialized	Crushed, or rarely tangen- tially elongate, thick- walled

Table 1. Continued.

Characters	Canellaceae	<i>Takhtajania</i>	Other Winteraceae ⁶
References	Corner (1976), Parmeswaran (1961, 1962)	Present study	Bhandari (1963), Bhandari & Venkataraman (1968), Corner (1976), De Boer & Bouman (1974), Prakash et al. (1992), Sampson (1963), Smissen (1993), Swamy (1952), Vink (1970, 1977)

Abbreviations: ii, inner integument; oi, outer integument.

¹ Ovules of Canellaceae are described as anatropous (Netolitzky, 1926; later authors). However, a drawing of a longitudinal section of an ovule of *Warburgia stuhlmannii* Engl. (Parmeswaran, 1962, fig. 25 on p. 173) suggests that the ovule is campylotropous rather than anatropous.

² According to Corner (1976: 86), the description of Parmeswaran (1961) suggests that the large seed of *Cinnamosma* appears to be pachychalazal, but this must be confirmed.

³ According to Corner (1976: 86), “Baillon described a vestigial aril round the hilum of *Canella*, but later authors have not reported it.”

⁴ According to Parmeswaran (1961), *Cinnamosma* (*C. macrocarpa* and *C. madagascariensis*) has ruminant processes in seed coats, which are not known in *Canella*, *Cinnamodendron* (including *Capsicodendron*), and *Warburgia*.

⁵ Based on earlier observations, Corner (1976: 86) noted that the exotesta is composed of sclerosed cells (except *Cinnamosma*), and that the seeds appear exotestal. The structure of the seed coat of Canellaceae has been studied very poorly, and more detailed study of the seed coat is needed for critical comparison.

⁶ The following taxa have been studied for some or part of the embryological characters of the genera of Winteraceae other than *Takhtajania*: “*Belliolum haplopus*” (B. L. Burt) A. C. Smith (Corner 1976), *Drimys* (*Tasmannia*) *piperita* Hook. f. (Corner, 1976), *D. winteri* (Bhandari & Venkataraman, 1968; De Boer & Bouman, 1974), *Pseudowintera colorata* (Raoul) Dandy (Bhandari, 1963; Corner, 1976), *P. axillaris* (J. R. Forst. & G. Forst.) Dandy (Sampson, 1963), three species of *Tasmannia* (Prakash et al., 1992), *Zygozylum bailloni* Tiegh. (Swamy, 1952), and *Z. stipitatum* Baill. (syn. *Exospermum stipitatum*) (Smissen, 1993). Unless otherwise stated, embryological features presented above are common to all the taxa studied.

⁷ The presence of an obturator is reported in all three species of *Tasmannia* studied by Prakash et al. (1992) but is not clear in other genera.

⁸ According to Corner (1976: 282) in “*Belliolum haplopus*” the micropyle is formed by the endostome and the exostome. This is reiterated by Johri et al. (1992: 242), who state that “in *Zygozylum* both the integuments are concerned” in the formation of the micropyle. However, there is no clear evidence for this, and all other literature sources available for this character in Winterceae indicate that the micropyle is formed by the inner integument alone and is covered by the outer integument (testa) after fertilization.

cap. Cells of the nucellus remain around the mature embryo sac (Fig. 15). An obturator is formed near the micropyle (Fig. 15). A hypostase is not formed.

INTEGUMENTS

The ovule is bitegmic, having an inner and an outer integument (Figs. 15–18). Neither the inner nor outer integument are multiplicative. The inner integument is 3-cell-layered (Fig. 18) from the beginning to older stages of development except at the apical part where it is about 5- to 7-cell-layers thick (Fig. 15). Some cells of the inner epidermis of the inner integument may, however, divide in places to increase the thickness, so that the inner integument is 4-cell-layered in places. The outer integument is 4- to 5-cell-layered from the beginning to older stages of ovules (Fig. 18).

By the fertilization stage the inner integument always develops beyond the outer integument to

cover the tip of the nucellus, so that the micropyle is formed by the inner integument alone (Figs. 15, 17). However, after fertilization, the testa (developed outer integument) develops further and reaches the tip of the tegmen (developed inner integument) (Figs. 19, 20). Therefore, when looked at in seeds, the micropyle appears to have been formed by both the inner and the outer integument.

ENDOSPERM AND EMBRYO

Fertilization is porogamous. Endosperm formation *ab initio* is of the Cellular type. No free endosperm nuclei have been observed in young seeds. Compared to the whole size of the nucellus, which is enlarged after fertilization, the embryo sac composed of cellular endosperm is small and narrow (Figs. 20, 21). In nearly mature or the oldest seeds available, the endosperm is positioned in the center

of the seed and is surrounded by a massive nucellar tissue, which appears to be degenerating (Fig. 19).

We did not examine embryogenesis in detail in this study, but fragmentary observations of early and late embryogenesis indicate that it proceeds normally to form a globular embryo (Fig. 21). In the nearly mature or oldest seeds available, we could not observe a dicotyledonous embryo. The seeds seem to be released from a fruit before the globular embryo develops into a dicotyledonous stage.

SEED AND SEED COAT

Nearly mature seeds are ellipsoid and somewhat angular (Figs. 19, 22) without any appendages such as an aril or a wing. The seed coat is formed by both the tegmen and the testa. Both the tegmen and the testa do not increase their thickness after fertilization. The tegmen is 3- to 4-cell-layers thick, and the testa is 4- to 5-cell-layers thick (Fig. 25). As the seed develops, cells of the exotesta radially elongate to assume a palisadal structure, while 3 to 4 underlying cell-layers of the mesotesta and the endotesta are rectangular in shape and tanniniferous (Figs. 25–27). On the other hand, none of the cell-layers of the tegmen exhibit any particular specialization and probably degenerate or collapse except at the micropylar part. Cells of the micropylar part of the tegmen are variously enlarged and thick-walled to form a persistent cap-like structure (Fig. 20). The seed coat is thus exotestal (for terminology of seed coat types, see Corner, 1976; Schmid, 1986).

DISCUSSION

In Table 1 embryological features of *Takhtajania* are summarized in comparison with those of the other Winteraceae as well as of the Canellaceae. Embryologically *Takhtajania* agrees well with the four other genera of Winteraceae (*Drimys*, *Pseudowintera*, *Tasmannia*, and *Zygogynum* s.l.). No particular characters suggest the distinctness of *Takhtajania* from the other Winteraceae and its basal position within the family. The embryological features of the family are summarized as follows.

Anther tetrasporangiate; anther wall development of the Basic type (unknown in *Takhtajania*); the anther epidermis becomes collapsed; the endothecium, the outermost cell-layer of the middle layers, and occasionally part of the connective tissue developing fibrous thickenings; other middle layers degenerating, and tapetum glandular; tapetal cells 2-nucleate; cytokinesis in meiosis simultaneous; the predominant shape of microspore tetrads tetrahedral; mature pollen grains 2-celled.

Ovule anatropous, bitegmic, and crassinucellate; archesporium 1-celled; parietal tissue 5–6 cells thick, tetrads of megaspores linear or T-shaped; mode of embryo sac formation of the Polygonum type; antipodal cells ephemeral; the mature embryo ellipsoid and positioned at the upper region of an enlarged nucellus; 2-cell-layered nucellar cap formed; hypostase not differentiated; an obturator formed; ovule or seed not pachychalazal; inner integument 3(–4) cells thick, and outer integument 4–5 cells thick; both integuments not multiplicative; vasculature absent in both the integuments; endothelium not formed; micropyle formed by the inner integument alone, but covered by an exostome after fertilization.

Fertilization porogamous; endosperm formation of *ab initio* Cellular type; mode of embryogeny of an undetermined type (in *Drimys winteri* J. R. Forst. & G. Forst.). Mature seeds albuminous with a very small embryo; seed coat exotestal, having lignified palisadal exotestal cells to form the most specialized mechanical structure; cells of mesotesta and endotesta little specialized or crushed but rectangular and tanniniferous in *Takhtajania*; tegmen usually crushed.

COMPARISONS WITH CANELLACEAE

Based on embryological data that is available for Canellaceae, the Winteraceae resemble Canellaceae in general, including having an exotestal seed coat (Table 1). Based on the presence of lignified exotestal cells (except in *Cinnamosma*), Corner (1976: 86) stated that the seeds of Canellaceae appear exotestal and indicate alliance with the Winteraceae. In addition, according to Huber (pers. comm. in Kubitzki, 1993), seeds of *Canella alba* Nees are exotestal, with a collapsed tegmen and nucellus, abundant and thin-walled endosperm free of starch, and a small and slender embryo, and they agree with those of Winteraceae (and Illiciales). However, information on the seed coat structure of Canellaceae is still extremely limited for critical comparison. Although the seed coat structure of several species of *Canella* and *Cinnamosma* has been briefly summarized (Corner, 1976), its development has never been documented. Therefore the exact structure of any species of the Canellaceae is not clear enough to verify how the seed coat structure of the Winteraceae resembles or is different from that of Canellaceae. Nor can we clarify whether or not the two families share exactly distinct seed coat structure from that of related taxa such as Piperales sensu lato (Qiu et al., 1999). Canellaceae need further detailed studies of these features.

Despite the limited data available for the Canellaceae, the whole family Winteraceae is clearly distinct from it, and all the five genera of the family share a few characteristic features that are not found in Canellaceae. For instance, in Winteraceae fibrous thickenings occur in the outermost one of the middle layers (and occasionally even in part of the connective tissue) as well as in the endothecium, while they occur only in the endothecium in Canellaceae; the micropyle is formed by the inner integument alone in Winteraceae, but is formed by both the inner and outer integuments in Canellaceae; the exostome is formed after fertilization in Winteraceae and not by the fertilization stage as in Canellaceae; ovules are anatropous in Winteraceae but campylotropous in Canellaceae; seeds of Winteraceae have a persistent micropylar part of the tegmen composed of variously enlarged, thick-walled cells, which is not reported in Canellaceae; the exotesta is palisadal and formed by radially enlarged, lignified exotestal cells in Winteraceae but not palisadal in Canellaceae. These distinctive embryological features support the coherence of the Winteraceae including *Takhtajania* and highlight the distinctness of the Winteraceae from the Canellaceae.

As discussed above, there is no embryological evidence to distinguish *Takhtajania* from the remainder of the family. In other words, Winteraceae are a well-defined group embryologically. Ancestral Winteraceae date back to the Barremian stage of the Early Cretaceous in tropical Northern Gondwana, and their descendents migrated from there to the southern temperate zone and eventually to the current distribution areas (Doyle, 2000 this issue). However, despite its modern widespread distribution, the family has been little diversified in embryological characters since it diverged from a common ancestor with Canellaceae.

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